Communication

Effects of Atmospheric CO_2 Enrichment on Photosynthesis, Respiration, and Growth of Sour Orange Trees[1]

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ABSTRACT

Numerous net photosynthetic and dark respiratory measurements were made over a period of 4 years on leaves of 24 sour orange (*Citrus aurantium*) trees; 8 of them growing in ambient air at a mean CO_2 concentration of 400 microliters per liter, and 16 growing in air enriched with CO_2 to concentrations approaching 1000 microliters per liter. Over this CO_2 concentration range, net photosynthesis increased linearly with CO_2 by more than 200%, whereas dark respiration decreased linearly to only 20% of its initial value. These results, together with those of a comprehensive fine-root biomass determination and two independent aboveground trunk and branch volume inventories, suggest that a doubling of the air's current mean CO_2 concentration of 360 microliters per liter would enhance the growth of the trees by a factor of 3.8.

Increasing the atmospheric CO_2 concentration to which plant leaves are exposed has long been known to increase their net photosynthetic rates (5, 14). More recently, it has been shown to decrease their dark respiratory rates (1, 3, 4). Little is known about the long-term consequences of the combination of these two effects for the growth and development of trees. Hence, we conducted a tree experiment wherein net photosynthesis and dark respiration responses to atmospheric CO_2 enrichment were monitored over a period of 4 years and used to predict net annual productivity. This communication summarizes our results and compares them with three separate determinations of above- and below-ground growth made after 2, 2.5, and 3 years of continuous exposure of the trees to different concentrations of atmospheric CO_2.

MATERIALS AND METHODS

Various aspects of the overall experiment have been described previously (9, 10, 12). The experiment was initiated in July of 1987, when eight sour orange tree (*Citrus aurantium* L.) seedlings were planted in the ground at Phoenix, Arizona, and surrounded in pairs by transparent walls of clear plastic

film. Beginning in November of that year, half of the open-top enclosures were supplied with a continuous bottom-to-top flow (4 volume changes/min) of air enriched, in the mean, with an extra 300 μL of CO_2/L of air (μL/L) by means of perforated plastic tubes located just above the soil surface, whereas the other half of the chambers were similarly supplied with a flow of ambient air.

In March of 1991, 16 new sour orange tree seedlings were planted in the ground and surrounded in pairs by eight identical enclosures. In this case, however, two of the enclosures were maintained at the ambient CO_2 concentration, whereas two of them received, in the mean, an extra 150 μL/L, two of them an extra 300 μL/L, and two of them an extra 450 μL/L of CO_2. Except for this one difference, all of the trees have been treated identically since the experiment's inception. Also, the trees have been irrigated and fertilized to preclude the development of both water and nutrient stresses.

Net photosynthetic and dark respiratory measurements were both made with LI-6200 portable photosynthetic systems (Li-Cor Ltd., Lincoln, NE), the cuvettes of which were clamped onto attached, fully-expanded, outer-canopy leaves for periods of approximately 30 s/measurement. The first measurements were made in the second year of the original (hereafter "large") tree study. These were daylight-only measurements. Similar data were obtained in 1990 and 1991 (years 3 and 4 of the large tree experiment and year 1 of the "small" tree experiment). The most recent year was also the period of most of our dark respiratory measurements on both sets of trees.

Although measurements were made over a number of different time intervals, the period from 0900 to 1600 hours local time was common to all net photosynthetic runs, and the period from 2100 to 0100 hours was common to all dark respiratory runs. In the first year of data acquisition (1989), measurements were made every hour during a run, whereas in all subsequent years measurements were made every hour and a half. At each of these measurement times, either two or three leaves of each tree were sampled, *i.e.* had their net photosynthetic or dark respiratory rates determined as described above, and the results from all the trees within a given treatment were averaged together. Finally, 0900- to 1600-hour net photosynthetic and 2100- to 0100-hour dark respiratory averages were determined for each measurement run, along with corresponding averages of CO_2 concentrations measured within the LI-6200 leaf chamber at the time of the photosynthetic and respiratory measurements.

Throughout the 3-year period of data acquisition, measurements were made in every month of the year. Air temperature variability among the different seasons thus had a large impact on the absolute rate of dark respiration, whereas variations in air temperature and solar radiation both affected the absolute rate of net photosynthesis. The resulting scatter in our measurements of net photosynthesis and dark respiration greatly obscured the effect of the different CO_2 treatments. Hence, to remove the influences of these two confounding factors and isolate the CO_2 effect, we normalized the net photosynthetic and dark respiratory data, deriving relative (dimensionless) rates of these two processes as follows.

First, the actual value of each CO_2 treatment's mean rate of net photosynthesis or dark respiration for a specific measurement run, expressed as μmol CO_2 exchanged/m² of leaf surface/s (μmol m^{-2} s^{-1}), was plotted against the corresponding mean CO_2 concentration of that treatment and run. The two (large tree study) or four (small tree study) data points thereby derived for each measurement run were then connected by straight lines, and the actual rate of net photosynthesis or dark respiration determined from this relationship to pertain to a CO_2 concentration of 650 μL/L was divided into each of that run's mean actual rates of net photosynthesis or dark respiration. Finally, the relative (dimensionless) numbers thereby obtained, which are to be compared to a value of unity at the arbitrarily chosen CO_2 concentration of 650 μL/L, were plotted as shown in Figure 1, where all of our results are combined into single plots of relative net photo-

synthesis and dark respiration versus atmospheric CO_2 concentration.

RESULTS AND DISCUSSION

The data of Figure 1 suggest that there were no major changes in the relative photosynthetic or respiratory responses of the leaves of the sour orange trees to atmospheric CO_2 enrichment over the 4 years of the experiment. This lack of any inhibition of photosynthesis with long-term exposure to elevated CO_2 is in harmony with the results of recent studies that have shown the often observed downward regulation of photosynthesis and growth at high CO_2 levels to be due to experimental protocols that result in restricted root growth (2, 16, 17). They also indicate that over the range of CO_2 variability encountered in our experiment (350 to 1000 μL/ L), the photosynthetic and respiratory responses to atmospheric CO_2 enrichment were linear. This observation, too, is contrary to what has historically been observed, but few prior studies of this nature have dealt with trees whose roots have been anchored in the undisturbed soil of the natural environment (13). There is also reason to believe that trees may respond differently from other plants in this regard. In the case of the leaves of the sour orange tree, for example, it has been shown that their stomatal conductance is rather insensitive to atmospheric CO_2 enrichment (8), and it could well be that it is the CO_2-induced decrease in stomatal conductance of most other plants (15) that causes their photosynthetic

Figure 1. Normalized, and hence dimensionless, net photosynthetic and dark respiratory rates of typical outer-canopy sour orange tree leaves relative to their values at an atmospheric CO_2 concentration of 650 μL/L versus atmospheric CO_2 concentration. Data for years 2 through 4 were derived from the large tree study initiated in 1987, whereas data for year 1 came from the small tree study initiated in 1991.
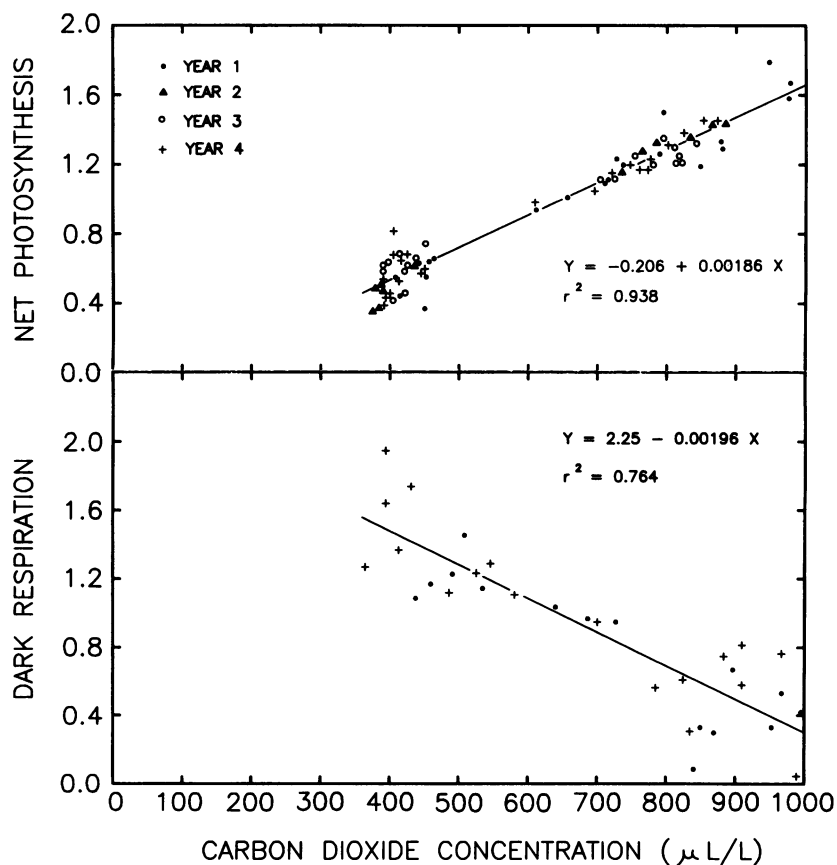
response to atmospheric CO_2 enrichment to gradually level off at high CO_2 contents. Where such a response is lacking, net photosynthesis may increase linearly with atmospheric CO_2 to much higher concentrations.

Our experimental results can be used to make a rough estimate of relative net annual growth stimulation due to atmospheric CO_2 enrichment. We begin with our observed annual averages of actual net photosynthetic and dark respiratory rates: 4.40 and −1.50 $\mu mol\ m^{-2}\ s^{-1}$, respectively, which pertain to a CO_2 concentration of approximately 400 $\mu L/L$. Then, from the relative responses of Figure 1, we determine the annual averages of actual net photosynthetic and dark respiratory rates at 700 $\mu L/L$ to be 8.96 and −0.90 $\mu mol\ m^{-2}\ s^{-1}$. For equal lengths of light and dark periods, the net CO_2 sequestration on a 24-h basis thus becomes 4.40 − 1.50 = 2.90 $\mu mol\ m^{-2}\ s^{-1}$ at a CO_2 concentration of 400 $\mu L/L$ and 8.96 − 0.90 = 8.06 $\mu mol\ m^{-2}\ s^{-1}$ at a CO_2 concentration of 700 $\mu L/L$. Hence, the relative net annual growth stimulation provided by a 400 to 700 $\mu L/L$ increase in the CO_2 content of the air is calculated to be 8.06/2.90 = 2.78.

An exacting test of the validity of this result is provided by the results of three separate and independent studies of the actual growth of the large trees, which have been continuously maintained at CO_2 concentrations of approximately 400 and 700 $\mu L/L$. In the first (12), a comprehensive inventory of all above-ground tree parts conducted at the end of the second growing season revealed that the total trunk plus branch volume of the trees receiving the extra 300 $\mu L/L$ of CO_2 was 2.79 times greater than that of the trees growing in ambient air. In the second study (9), direct sampling of the trees' root zones midway through the third growing season revealed the CO_2-enriched trees to have 2.75 times more fine-root biomass than the ambient-treatment trees. And in the third study (11), a second comprehensive inventory of all above-ground plant parts conducted at the conclusion of 3 full years of the experiment showed the CO_2-enriched trees to have 2.90 times more trunk, branch, and fruit-rind volume than the trees growing in ambient air. The mean growth enhancement factor of these three studies is 2.81, which is nearly identical to our calculated value of 2.78.

Based upon this correspondence, we calculate that for a doubling of the current mean global atmospheric CO_2 concentration of 360 $\mu L/L$, the growth and CO_2 sequestering ability of common sour orange trees would be increased by a factor of 3.80. In view of the magnitude of this response and its obvious importance to global carbon cycling, it is imperative that other trees be studied in a similar manner, as recent analyses of the annual cycle of the air's CO_2 content suggest

that most trees should respond similarly (6, 7). Higher atmospheric CO_2 concentrations should also be employed to determine the ultimate limit of this impressive growth response.

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